

Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary

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Abstract

Juvenile pelagic fishes are integral members of many coastal river communities. Many of these systems are strongly influenced by variable wind stress and freshwater inputs that can increase heterogeneity in estuarine habitat for fishes. We use mobile sonar surveys within the Neuse River Estuary System, NC, USA to assess the distribution and behavioral patterns of juvenile anchovies, *Anchoa* spp. 25–65 mm TL, over a broad range of spatial scales in relation to diel and seasonal changes in water quality including stratification, hypoxic events and copepod distribution. Results from our study indicate that episodic stratification-induced hypoxic events can reduce suitable habitat volume for anchovies by more than 50%. Furthermore, our sampling suggests that hypoxia causes spatial separation between plankton and the grazing fishes. Under stratified oxygen conditions, we observe higher densities of copepods in hypoxic bottom water. Finally, we report that reductions in available habitat caused an increase in local densities of fishes and may result in increased competition for resources. These spatially explicit data are critical for developing trophic dynamic models that predict the response of fish communities to natural and anthropogenic impacts on the system.

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1. Introduction

Estuary-dependent fishes occupy spatially complex and temporally dynamic habitats during portions of their life-history. Juvenile stages of numerous commercially and ecologically important fish species rely on the estuarine habitats as a nursery for rapid growth and as a refuge from predation (Minello, 1999). Several factors influence the spatial distribution of juvenile fishes in estuaries. These factors can be broadly categorized as abiotic factors, such as salinity, temperature, pH, dissolved oxygen (DO), and benthic structure, and biotic factors, such as prey availability and predator abundance.

Numerous studies have documented relationships between the abundance of juvenile estuarine fishes and the presence and complexity of physical structure such as oyster reefs, sea grasses, and salt marshes (Minello, 1999). DO is an

additional abiotic factor that can structure estuarine fish populations in estuaries (Breitburg, 1992; Howell and Simpson, 1994). Several studies have focused on the effects of low DO (hypoxia) on the distribution of demersal fishes (Pihl et al., 1991; Howell and Simpson, 1994), but only a few studies have been devoted to an understanding of the interactions between hypoxia and predator-prey relationships (Pihl et al., 1992; Keister et al., 2000). We are not aware of any studies that have focused on the interactions of DO and prey dynamics on the distribution of juvenile pelagic fishes in shallow estuaries; however, recent work has documented relationships between larval anchovies and zooplankton and bottom-layer DO (Keister et al., 2000). Dominant pelagic fishes such as anchovies, *Anchoa* spp., and menhaden, *Brevoortia* spp., comprise the majority of the fish biomass in many estuaries of eastern North America. These species serve important commercial (in the case of menhaden) and ecological roles as prey resources for commercially important piscivores. It may be counter-intuitive to suppose that pelagic fish populations would be impacted by hypoxic events that occur in the

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hypolimnion. As a result, previous studies examining the distribution of pelagic fishes in US estuaries have focused primarily on their distribution in relation to biotic factors, and more specifically prey fields such as zooplankton patchiness and phytoplankton dynamics (Peebles et al., 1996; Friedland et al., 1989).

The pelagic environment of shallow aquatic systems presents a challenge for sampling fish communities. Previous assessments of the distribution of estuarine fishes in relation to habitat quality have primarily used trawls, which are restricted to coarse spatial scales and do not adequately sample the near surface. Fisheries hydroacoustics provides an improved, non-invasive method of collecting information on the distribution of fishes within aquatic habitats, over a continuum of spatial scales throughout the water column (MacLennan and Simmonds, 1992). Furthermore, in shallow aquatic habitats (<10 m), depth-discrete active or passive sampling gear has proved ineffective at determining the distribution of small fishes in the vertical dimension (Taylor and Rand, unpublished data). Split-beam hydroacoustic technology now gives us the ability to describe 3D distribution patterns of estuarine fishes and to better assess the relationship between fish populations and the spatially complex, physicochemical environment.

The aim of this paper is to characterize the spatial structure of fish distribution as a function of water column stratification and hypoxia in the lower water column. Understanding the spatial structuring of the grazing fishes will lead us to better estimates of grazing impact and trophic efficiencies in estuarine food webs impacted by adverse water quality.

2. Methods

Surveys were conducted in the lower Neuse River Estuary (NRE), NC, USA (Fig. 1). The Neuse River is one of two major rivers that provide freshwater input into the Pamlico Sound, the largest lagoon-type estuary in the eastern US. A single transect was sampled at night on two dates. The first date, 26 June 2001, was during a period of severe density stratification and the hypolimnion was hypoxic ($\text{DO} < 2 \text{ mg O}_2 \text{ l}^{-1}$). The second date, 2 August 2001, was during a period when the water column was mixed and oxygen was nearly homogeneous throughout.

The survey was conducted between 23:30 and 00:30 on both occasions. We used a 200-kHz HTI Model 241 split-beam echosounder coupled with an elliptical ($4^\circ \times 10^\circ$ nominal beam dimension) transducer and a circular (15° nominal beam dimension) transducer to assess abundance of fish in the vertical and horizontal dimensions from the surface to within 0.25-m from the bottom. The elliptical transducer was oriented perpendicular and lateral to the vessel path and sampled the top 1.5-m of the water column from 10 to 30-m athwart ship. The circular transducer was oriented vertically and sampled from 1-m below the surface to within 0.25 m from the bottom. Vessel speed was constant at about

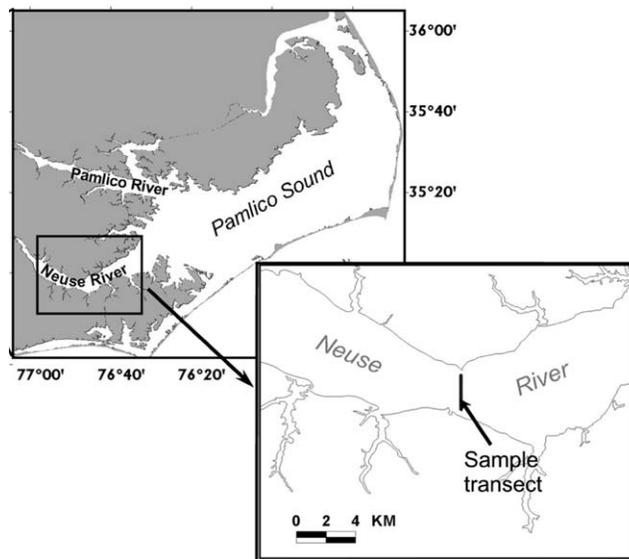


Fig. 1. Sample transect in the lower Neuse River Estuary, NC, USA.

1.8 m s^{-1} . A ping rate of 10 pulses s^{-1} was multiplexed between the two transducers, resulting in 5 pulses s^{-1} to each transducer. Each sampling occasion was preceded by an in situ system calibration using a tungsten-carbide reference sphere of known target strength placed greater than 5-m from the transducers. Gain parameters were adjusted accordingly based on calibration results. Returned acoustic signals were simultaneously adjusted for spreading loss by applying $40\text{-log } R$ and $20\text{-log } R$ time-varied gain for split-beam and echo-integration processing, respectively. The data were processed in real-time for split-beam and echo-integration (HTI DEP v. 3.53, HTI Seattle, WA, USA) and stored on a laptop computer for later data analyses.

The acoustic survey coincided with a sampling of water quality using a data logger (YSI Model 6600) at 4–5 stations along the transect. The data logger recorded temperature, salinity, and DO at 0.1-m increments through the water column. All parameters were interpolated along the cross-section of the river to provide a visualization of the water quality observed during the hydroacoustic sampling. Discrete zooplankton samples were taken at 2 or 3 depths at each station using a 30-l Schindler-Patalis plankton trap fitted with a $63 \mu\text{m}$ mesh net. Samples were preserved in 2–5% buffered formalin, and subsamples were counted for juvenile and adult (copepodite) stages in the laboratory. Densities of copepods were calculated and reported in ind. m^{-3} . To verify fish size and species composition in the surveyed area, we sampled 18 stations using a surface trawl (1.2 m width, 0.7 m height, 3.5 m length, 3.2 mm knotted mesh) that was towed between two small boats and targeted the top 1 m of the water column. Results from this survey indicated that anchovies, *Anchoa* spp., comprised over 98% by number of the fishes encountered.

Acoustic data were processed using split-beam and echo-integration analyses. Split-beam analysis was used to determine the acoustic size (target strength) of individual fish

targets in decibels. Using equations for clupeiform species, target strengths were converted to approximate fish size and to wet weight (Foote, 1986; Taylor, unpublished data). Echo-integration provided a measure of relative density that can be converted to absolute density by scaling the integrated acoustic signal within a cell by the average target size within the cell. For this study, down-looking echo-integration data were divided into cells approximately 25-m long by 0.5-m deep from 2.0-m below the surface to the bottom. The side-looking integration data were divided into cells 25-m long and 1.5-m deep and was calculated as the average voltage return from 10 to 30-m athwart ship. Average target strength was calculated for each cell and during each sampling occasion. Only fish targets between -57 and -43 dB (ca. 20–100 mm TL) were used for the split-beam and echo-integration analyses, representing the range of fish sizes sampled in the surface trawl samples. All targets were assumed to be *Anchoa* spp. based on the surface trawl samples. Densities, measured in no. m^{-3} and g m^{-3} , were calculated for each cell by scaling the mean voltage returned from the ensonified volume by the average fish size calculated from split-beam analysis and verified using the surface trawl survey.

2.1. Data visualization and statistical analyses

Summary statistics for fish size and densities were computed for each of the surveys. Echo-integration data were analyzed for large- (trend) and small-scale (autocorrelation) spatial structures. We used a generalized additive model (GAM) to characterize the spatial trend in the data for the transect on each sampling occasion. Distance-along-transect (in meters) and depth in the water column (in meters) were used as covariates to explain the variability in root-transformed echo-integrated density. The root-transformation of the echo-integration data appeared to best normalize the data, since the data were highly skewed and there were many zero-densities in the dataset. A stepwise regression technique was used to optimize the degrees of freedom used for each covariate in the smoothing functions of the GAM. Predictions from the GAM and its residuals were plotted to examine them for normality. Approximate r -squares were calculated to determine the amount of variability explained by the spatial covariates. Residuals from the GAMs were then analyzed for the remaining spatial structure by calculating the semivariance as a function of the distance between measures (Cressie, 1993). The behavior of the empirical variogram suggested that a Gaussian model would best fit the data. The range, sill and nugget parameters were estimated using non-linear least squares procedures to estimate the spatial extent of correlation, the range parameter of the theoretical variogram. Significant model variogram parameters were compared between the two surveys to assess differences in the spatial patterns of densities that may be explained by the differences in habitat quality between the two sampling occasions. All statistical analyses were performed using S-plus (v. 6.0, Insightful Corporation, 2001).

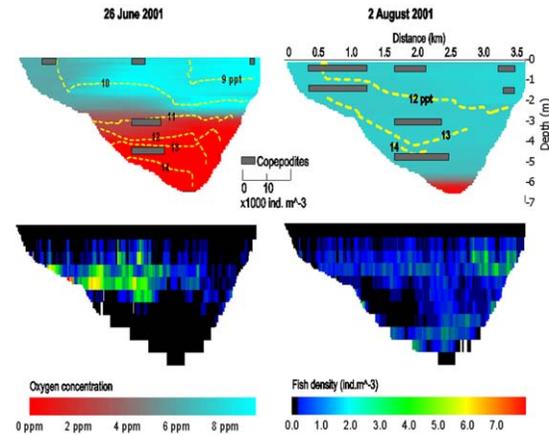


Fig. 2. Cross section of the transect sampled in June and August 2001. Viewing direction is toward the west with the south on the left and north on the right of each plot. Vertical and horizontal dimensions of each plot are according to axes in top right panel. Interpolations of water quality (top panels) are represented by salinity (broken yellow lines) and DO (color bar at lower left). Copepod densities are represented by gray bars at sample locations and are proportional to the scale inset. Echo-integrated fish density is represented in the lower panels. Densities ranged from 0 to 8 fish m^{-3} represented by a color spectrum (lower right).

3. Results and discussion

Patterns in water quality were quite different between the two sampling occasions with respect to DO and salinity.

3.1. June sampling

During the night of 26 June 2001, the transect was stratified with the pycnocline (12–13 ppt) and thermocline (28.0–27.0 °C) at a depth of 3-m and $>50\%$ of the water column under hypoxic conditions (Fig. 2). Hypoxic events during the late-spring to early-fall in the Neuse River were strongly correlated with stratification caused by spring freshwater input, early-spring organic matter decomposition, and the magnitude and direction of wind stress (Borsuk et al., 2001; Paerl et al., 1998). Low wind stress before the June sampling contributed to density stratification, which was caused primarily by salinity differences between the intruding high salinity water from the Pamlico Sound and net downstream flow of the freshwater from the Neuse River. Copepodites that were sampled concurrently during the hydroacoustic survey indicated higher densities at and below the pycnocline in DO concentrations lethal to larval anchovies (Fig. 2; Breitburg, 1994). This pattern was in contrast to the observations in the Chesapeake Bay, where copepodites avoided bottom-layer $\text{DO} < 3 \text{ mg O}_2 \text{ l}^{-1}$ (Keister et al., 2000). Large copepodites were the preferred prey of the anchovies (Peebles et al., 1996) and represented the majority of the stomach contents of anchovies captured during this study (Taylor and Rand, unpublished data).

Average estimated fish size for June was 32.8 ± 0.6 mm TL (mean \pm SE, Table 1) and corresponded well with our surface trawl sampling in the region, which averaged 35 ± 1 mm TL. The distribution of June density values was highly

Table 1
Summary of fish size and distribution of echo-integrated densities

Date	Estimated TL (SE) (mm)	Mean density (SE) (no. m ⁻³)	Median density (no. m ⁻³)	Min/Max density (no. m ⁻³)	Biomass (g)
26 June 2001	32.8 (0.6)	0.50 (0.04)	0.04	0/8.31	809
2 August 2001	30.3 (0.3)	0.66 (0.02)	0.50	0/3.42	1054

skewed and contained many zeros. Density values along the transect averaged 0.50 fish m⁻³ (median = 0.04 fish m⁻³) and ranged from 0 to 8.31 fish m⁻³ (Table 1). High variability and frequent zeros were common in the surveys of pelagic species (Freon and Misund, 1999).

The GAM covariates of horizontal distance and depth explained 60.5% of the variability in the density distribution in June. There was a weak effect of horizontal distance, with higher densities toward the middle of the river (Fig. 3). This pattern may be better explained by the effect of depth on the vertical distribution, especially in the middle of the river. The results from the GAM indicated a significant positive relationship of fish density and depth from the surface to approximately 3-m depth (Fig. 3). Vertical density distributions generally matched the pattern of oxygen stratification with very few fish encountered below 3.5-m. Larval stages of anchovies in the Chesapeake Bay were also observed to avoid hypoxic waters (Breitburg, 1994). Our results also suggested that the fish were aggregating near the pycnocline. In larger ocean and coastal systems, the evidence of changes in vertical distribution was attributed to depleted oxygen in the lower water column. Mathisen (1989) reported changes in the maximum depth of anchoveta during extreme El Niño events that resulted in an oxygen depletion closer to shore. Further work is required to better characterize the movements of pelagic fishes that may help explain this pattern.

Presence of aggregations was further supported by the analysis of the spatial structure of the residuals of the GAM. Small-scale spatial correlation was present in the residuals to an estimated range of 400 m (Fig. 4). High degrees of correlation were especially evident from 20 to approximately

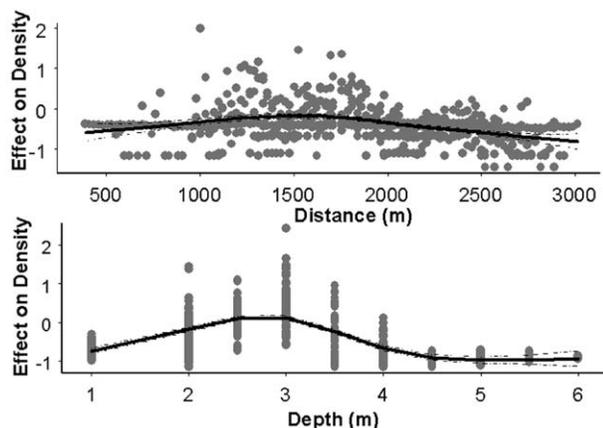


Fig. 3. GAM results for June 2001 fish density. Closed circles represent the residuals. Spline fit (solid line) is bound by 95% confidence intervals (dotted lines).

200-m lag distance. These small to medium sized patches can be seen in the data plotted in Fig. 1. We were surprised to see residual spatial structure in the data since other pelagic species that have been studied generally show disaggregate patterns during the night while shoaling or schooling during the day (reviewed in Freon and Misund, 1999). Dense aggregations may indicate that these fish were occupying microhabitats with high prey resources. Such high local densities of grazers, however, may lead to increased competition for resources, decreased feeding rates by individuals, and possible increases in activity costs. These mechanisms can lead to decreased individual growth rates and lower population production.

3.2. August sampling

Water quality sampling on 2 August 2001 showed a generally mixed water column with high DO down to approximately 5.5-m (Fig. 2). Just prior to this period, the NRE experienced moderate wind stress that served to mix the water column and bring oxygenated water to the hypolimnion. Zooplankton abundances were higher than those observed in June and were also generally homogeneous throughout the water column (Fig. 2).

Average estimated fish size for August was 30 ± 0.3 mm TL, and, as with sampling in June, corresponded well with our surface trawl samples, which averaged 31.8 ± 0.2 mm TL (Taylor and Rand, unpublished data). The distribution of August density values was not nearly as skewed as June

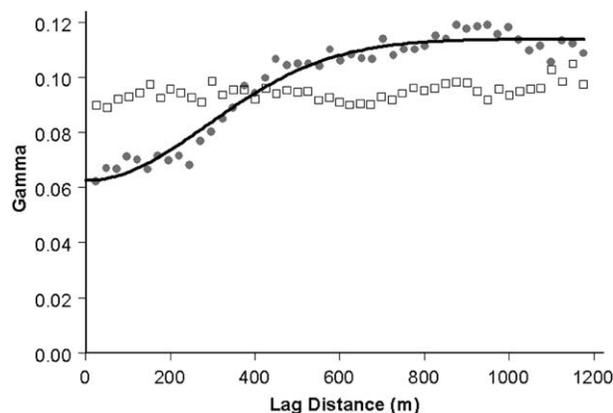


Fig. 4. Variogram plots from analysis of spatial structure of residuals from GAMs for June (closed circles) and August (open squares). Data points represent calculated semivariance (gamma) at lag distances along the x-axis. Dark line is a fitted theoretical variogram to the June data with parameters for the Gaussian model, range: 406.32, sill: 0.05, nugget: 0.06. No significant model was found for the August data.

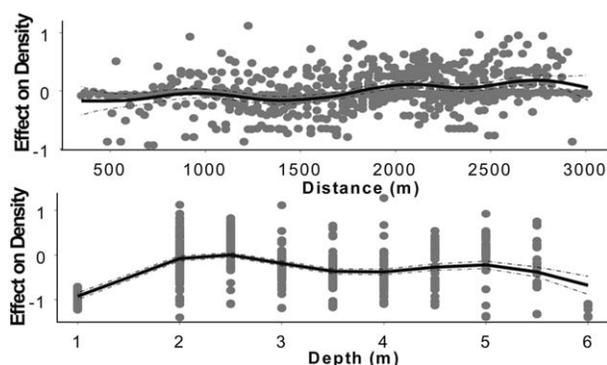


Fig. 5. GAM results for August 2001 fish density. Closed circles represent the residuals. Spline fit (solid line) is bound by 95% confidence intervals (dotted lines).

values and contained fewer zeros. Density values along the transect during August averaged 0.66 fish m^{-3} (median = 0.50 fish m^{-3}) and ranged from 0 to 3.42 fish m^{-3} (Table 1).

The GAM model for the August density distributions explained 48% of the variability in the data. In contrast to June, there was a weak positive effect of distance along the transect, with more fish present near the end of the transect (Fig. 5). This pattern was opposite to the trend in zooplankton abundances across the transect (Fig. 2), and may be a result of localized grazing effects on the plankton. Vertical distribution was also quite different from the pattern observed in June, with fish generally evenly distributed from 2-m to near bottom (6-m). The more uniform distribution of fish in the water column appeared to be a more typical pattern observed with nighttime acoustic data (reviewed in Freon and Misund, 1999), and served as a stark contrast to what we observed in June.

Unlike the results from the analysis of small-scale spatial structure in the June sampling, there was no spatial pattern in the GAM residuals for August (Fig. 4). The empirical variogram indicated a pure nugget effect, and neither the sill nor the range parameters of the model variogram were significant. With evidence of only a weak trend... “with the sentence” Given the prevalence of normoxia, and the overall higher densities and more uniform distribution of zooplankton prey during this sampling period (Fig. 2), we hypothesize fish exhibit a more uniform distribution throughout the system as a result of less restrictive limits on available oxygen and prey resources in the system. The apparent inverse relationship between grazing fish and zooplankton densities observed across the horizontal dimension may indicate how these grazing fishes may affect copepod dynamics through localized grazing pressure. This latter conclusion is speculative and requires further investigation.

4. Conclusion

Hydroacoustic data analyzed with modern statistical methods provides us with new insights into the environmental factors that structure the distribution of pelagic estuary-

dependent fish populations in shallow systems. These results represent the first reported efforts to quantify the spatial structuring of pelagic fishes in response to oxygen stratification in a periodically stratified estuary. Under stratified conditions, we found that fish form dense aggregations at night, in conditions when overall prey concentrations in the epilimnion were low. This suggests that fish may be depleting prey concentrations in the epilimnion or concentrating in prey patches that we cannot resolve with our current plankton sampling methods and argues for an approach where we can more closely match the scale and resolution of sampling of both fish and plankton communities. Future hydroacoustic sampling coupled with intense sampling of the zooplankton community will allow us to extend the analysis to important biotic processes, particularly with regard to better assessing the interactions of abiotic and biotic factors in determining the spatial distribution of pelagic fishes in estuaries. These data are important to develop trophic models that will predict population dynamics as a function of habitat quality. Physical models suggest that anthropogenic sources of nutrients increase the propensity of hypoxic events during periods of low wind stress (Paerl et al., 1998; Borsuk et al., 2001). Varying durations and severity of stratification and hypoxia will likely result in complex interactions between the zooplankton populations and the grazing fish community, the transfer of energy between the two trophic levels, and system-wide fish production.

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